THE ECOLOGIC FOLIAR ANATOMY OF SOME PLANTS OF A PRAIRIE PROVINCE IN CENTRAL IOWA

ADA HAYDEN

INTRODUCTION

While exact records of environmental factors such as edaphic features, temperature, light, water, and biotic relationships are essential in the determination of the character of plant habitats, such data serve merely as an introduction to the investigation of the adaptation or equipment of plants for living in specific locations. While certain external characteristics, such as small or dissected leaves, are associated with sun plants, and broad leaves with shade plants, histological study reveals in greater detail any modifications of the normal type of tissues which are known to perform special activities. That the activities pertaining to the life processes of the plant are closely associated with its use of water is a well known physiological fact, so that not only the available water of the habitat but that which the plant actually uses or what passes through it in the transpiration stream is an important indicator of its toleration of conditions peculiar to its particular habitat. Work has been done by Livingston, Bakke, Shreve, and others on the transpiration of plants, and Bakke (1) has proposed a classification of plants as xerophytes, mesophytes, or hydrophytes on the basis of transpiration, which it seems is a very exact indicator of the available water used. While indices of transpiration would no doubt be desirable in connection with a morphological study, and would probably throw some light on whether a special type of tissue were characteristic of a species because of reaction to habitat or because of ancestral influence, the observations reported in this paper are confined to the morphological phase alone.

SELECTION OF MATERIAL

Leaves and subterranean portions were chosen for examination since these organs are critical "indicators" of absorption and transpiration of water and therefore are more closely related to the regulation of the water supply than stems, which serve primarily as conductors. The plants selected were representative species of their habitats, *i. e.*, those species which were facies, or prominent in frequency or as to their vegetative perfection, for such plants may be regarded as instances of successful occupation of their respective environments.

Methods

Free-hand sections were made from typical mature leaves, usually selected from different plants, and from these the more representative sections were selected for mounts. After cutting, the sections were killed and fixed by immersion in hot alcohol, stained with a water-soluble safranin followed by haematoxylin, cleared in cedar oil and clove oil, and mounted in Canada balsam. Drawings of the leaves were made by camera lucida to a single scale of magnification. *Qualitative data have been sought rather than quantitative.* The thickness of the epidermis of leaves of one species as compared with the thickness of epidermis of another is not necessarily a positive or negative indicator of xerophytism, for one leaf may have trichomes plus a degree of thickness of epidermis found in the trichomeless leaf. Data concerning features regarded as "indicators" have been collected and relative proportions of tissues have been noted in individual plants.

Historical

While many physiologists are yet skeptical concerning the use of such terms as "reaction" of a plant to its habitat, "modification," or "adaptation," careful investigation has shown that species do change their structure under different environmental conditions, although these words have been somewhat inexactly used and perhaps more exact terms might be evolved. Whether certain histological characters are due to environment or to ancestral influence can be determined only by some histological knowledge of closely allied forms and some experimental evidence regarding one species placed under different conditions. Schimper (15), who has done extensive research of recognized excellence in histology, ecology, and plant geography, as well as some work in physiology, states: "All experiments have led to essentially similar results. External conditions which, either by diminishing the absorption of water or by accelerating its exit from the plant, disturb the equilibrium in a sense hostile to the plant, occasion, as a rule, the following deviations from normal structure: (1) Reduction of surface, the volume being assumed constant. (2) Diminution of intercellular spaces containing air. (3) Augmentation of vessels and sclerenchyma. (4) Lengthening of the palisade cells, frequent but not universal. (5) Increase in the thickness and amount of cutin of the outer wall of the epidermis. (6) Sinking of stomata. (7) Increased number of air-containing cells. (8) Supply of water-storing cells, such as double epidermis, aqueous tissue, mucilage cells.

Haberlandt (6) calls attention to two main principles of the anatomical structure of the photosynthetic system: (*a*) the principle of maximum exposure of surface, and (*b*) the principle of expeditious translocation.

The morphological structure of photosynthetic cells whose modifications are regarded as facilitating translocation are summarized by Haberlandt

under three systems of structure. In system 1, the photosynthetic tissue is itself responsible for the removal of synthetic products from the entire organ. In system 2, distinct tissues are set apart for photosynthesis and for translocation, the synthetic products being transferred directly from one to the other. In the third and most efficient system, the photosynthetic products are not transferred directly from photosynthetic elements to the different channels but pass first through special intermediary tissues.

Sachs has shown by experiment that starch is quickly removed from specialized parenchyma cells. Haberlandt has observed that the girdle type of palisade shows a very rapid elimination of starch.

There is apparently diversity of views regarding development of palisade parenchyma, some of which Miss Starr (18) in her study of the anatomy of dune plants summarized as follows: "Mrs. Clements (4) considered light the principal factor in the development of deep palisade. . . . Wagner reported that Alpine plants exposed to decreased transpiration did not show a reduction in palisade, and concluded that not transpiration but assimilation was more effective in producing that tissue. Pick (14) thought the elongated form of the palisade is ancestral, but that for a strong development light is necessary; Dufour (5) agreed with him in this respect. Stahl related palisade development to light. Eberdt thought increase in palisade development is caused by assimilation and transpiration working together, and that light in itself is never the cause that calls forth palisade parenchyma. Vesque and Viet (20) concluded from their experiments that light and dry air (accelerating transpiration) result in a greater development of palisade. Bonnier (3) adds temperature considerations to these two factors. Kearney (9) considers excessive transpiration accountable for both increased palisade and succulency. Heinricher related equilateral structure to the vertical position of leaves and thought it due to sunny and dry situations, dryness being secondary to strong illumination, as some plants growing in damp situations have equilateral leaves."

Solereder (19), who has compiled two comprehensive volumes on the systematic anatomy of the dicotyledons in which an enormous amount of data has been correlated, substantiates Schimper's views as to the anatomical indicators of xerophytism, and the reverse, but adds concerning the determination of adaptive features that these can be ascertained only by (1) examination of individuals of the same species from different habitats; (2) experimental treatment under definite conditions differing from those of the natural habitat; (3) the study of a larger group of plants undertaken in relation to the geographical area over which its members are distributed; and (4) comparative investigation. In speaking of the enumerated characters generally associated with xerophytic plants, such as thick cuticle, depressed stomata, etc., Solereder says that all these adaptations must not be supposed to be quite general, for if that were so, all plants which were subject to the same conditions would possess the same biological

structural features even if they belonged to the most widely separated groups. This is only exceptionally true. Experience shows that one species reacts in one way, other species in a different way, under the action of the same stimulus, but that the reaction is often of the same kind in plants belonging to the same phylum. Thus one species protects itself against desiccation solely by means of mucilage receptacles, another by the development of hypodermal aqueous tissue, a third by enlargement of epidermal cells, and others by two or more of these features. Reiche, Volkens, and others have shown that climate and habitat do not impress any one definite type of anatomical structure upon all the species of a certain geographical area. Species possess a definite plasticity which, however, may vary in degree and direction in individuals; in such cases we may find discrepancies between structure and external conditions. According to Vesque and Areschoug the leaves of Nelumbium bear stomata on the upper side only, just like floating leaves. This fact is drawn from the theory that Nelumbium is derived from an ancestral form possessing floating leaves and is supported by the results of physiological researches in which it has again been emphatically shown that the anatomical structure is the product of two factors—adaptation and heredity. The second factor, which sometimes becomes more noticeable than the first, allows us to employ biological structural features to a very considerable extent for systematic purposes.

Biological characters serve principally for the diagnosis of species. Within the same group of affinity, these characters are often identical in all those forms in which they appear; or they may be constant for groups of allied species, for genera, or for small orders. Biological characters may be divided into those which differ qualitatively and those which differ quantitatively; of these the former have the greater systematic value. The presence of hypoderm in a leaf is a more important fact than the number of layers of hypoderm. Abundant material of the same species from different habitats and cultural conditions should be compared.

Description of Leaves

Gramineae

Andropogon scoparius Michx.

Habitat: Dry soil; hill crests; slopes.

[1] Orientation and arrangement: Blade ascending, appressed to stem when young; opposite.

Gross structure: Lanceolate; blade glabrant except near sheath.

Histology (fig. 1, plate IX):

Outer walls of epidermis twice as thick as inner; bulliform cells prominent.

Parenchyma: Palisade cells concentric around the vascular bundles; spongy tissue between bundles; vascular tissue prominent.

Stomata small.

[1] The term *orientation* as here used refers to the plane in which the leaf blade lies, whether horizontal, vertical, or ascending.

Summary: The bulliform cells are prominent. The thickened outer walls of the epidermal cells are indications of water conservation. This plant not only grows in a dry habitat but has abbreviated roots.

Bouteloua curtipendula (Michx.) Torr.

Habitat: Dry hill crests and slopes.

Orientation and arrangement: Ascending; alternate.

Gross structure: Small lanceolate-linear; flat or involute; scabrous above; sometimes pubescent beneath.

Histology (fig. 2, plate IX):

Outer walls of epidermis about twice as thick as inner walls; upper epidermal cells terminating in barb-like points at intervals; lower epidermis with trichomes; bulliform cells prominent.

Mesophyll reduced, represented by a radial row of palisade cells around the bundles.

Vascular tissue prominent, including a row of large water-storing cells.

Stomata small.

Summary: The thickened epidermal cells prominent, bulliform cells well developed; the conspicuous vascular tissue and the reduced photosynthetic tissue are marked indicators of conservational facilities. Bouteloua lives in drier areas and has a more restricted habitat than *Andropogon scoparius*.

Muhlenbergia mexicana (L.) Trin.

Habitat: Damp soil; low land; alluvial basin.

Orientation and arrangement: Ascending; alternate; somewhat appressed to stem.

Gross structure: Lanceolate-linear; small; scabrous.

Histology: Homogeneous (fig. 3, plate IX).

Outer walls of epidermis slightly thicker than inner; cells terminating in barb occasionally; bulliform cells not prominent.

Parenchyma: Spongy in appearance; of roundish to oval cells compactly arranged.

Vascular tissue not prominent.

Stomata small.

Summary: This plant shows little tendency to conserve water. Vascular tissue is not so prominent as in grasses of drier habitats. Epidermis is not so specialized while photosynthetic tissue is fairly prominent.

Leersia oryzoides (L.) Sw.

Habitat: Alluvial basin; edge of swamp.

Orientation and arrangement: Ascending, somewhat appressed to stem; alternate.

Gross structure: Narrowly lanceolate; scabrous.

Histology: Homogeneous (fig. 4, plate IX).

Outer walls of epidermis slightly thickened; bulliform cells not prominent.

Vascular tissue fairly prominent.

Stomata small.

Parenchyma spongy; compact.

Summary: Water-conserving measures, though somewhat evident in the thickened outer wall of the epidermis and the differentiation of bulliform cells—are not so prominent as in *Andropogon scoparius* (fig. 4, plate IX) and *Bouteloua curtipendula* (fig. 2, plate IX), while photosynthetic tissue is better developed than it is in the leaves of the two last-named species.

Polygonaceae

Polygonum Muhlenbergii (Meisn.) Wats.

Habitat: Alluvial basin; wet soil and shallow water at edge of ponds. Not submerged.

Orientation and arrangement: Horizontal to ascending; petiolate.

Gross structure: Lanceolate to ovate; water form smooth; land form scabrous.

Histology: Bifacial (figs. 5*a* and 5*b*, plate IX).

Epidermis: Moderately thin-walled; slightly thicker on outer surface of water form; trichomes present on land form, also mucilagin us epidermal cells.

Stomata smaller on land than on water form.

Palisade parenchyma in two layers in both forms; the upper of irregular long cells, the lower of shorter and irregular cells; the land leaf is thicker than the water leaf, because the palisade parenchyma occupies 3/8 of the parenchyma space in the water form and 5/9 of the parenchyma space in the air form.

Spongy parenchyma about equally developed in both forms; loose.

Summary: These leaves indicate abundant water for needs with little provision for its conservation. The air leaf is a little thicker because of its increased thickness of the palisade, and its lower epidermis is equipped with trichomes and smaller stomata.

Ranunculaceae

Anemone cylindrica Gray.

Habitat: Dry, gravelly hill crests; dry, wind-swept.

Orientation and arrangement: Blade horizontal; radical leaves petiolate, involucrate leaves sessile.

Gross structure: Digitately cleft to parted; pubescent.

Histology: Bifacial (fig. 6, plate IX).

Epidermis with curved walls; outer walls about three times as thick as inner; large-celled compared with the parenchyma.

Stomata small; level with lower edge of epidermis.

Palisade parenchyma in 2 layers; slender; irregular; occupies 2/5 parenchyma space.

Spongy parenchyma small-celled; close; compact; about 3/5 the parenchyma space.

Summary: This leaf is equipped with trichomes, thick outer epidermal walls, and compact photosynthetic tissue.

Leguminosae

Amorpha canescens Pursh.

Habitat: Hill crests and dry hillsides.

Orientation and arrangement: Horizontal; petiolate; alternate.

Gross structure: Pinnately compound; hoary pubescent.

Histology: Subcentric (fig. 7, plate X).

Epidermis with approximately straight-sided cells; cells small; outer walls hardly thicker than the inner; trichomes present.

Palisade parenchyma in four layers graduated in size, longest on upper side; compact.

Spongy parenchyma absent.

Summary: The compact structure and the prominent trichomes show marked conservational features in accord with its specialized photosynthetic tissue. This plant, though living in dry situations, has a deep root which may reach a lower water table than the roots of some of its associates.

Baptisia leucantha T. & G.

Habitat: Alluvial basin; moist soil.

Orientation and arrangement: Horizontal or somewhat inclined; almost sessile.

Gross structure: Palmately 3-foliolate; leaflets wedge-shaped.

Histology: Subcentric (fig. 6*a*, plate X).

Walls of outer epidermis about three times as thick as inner; fairly large oblong cells with long axis horizontal.

Palisade parenchyma rather loose; cells medium-sized. Stomata slightly depressed.

Summary: The somewhat thickened outer wall of the epidermis and the slightly depressed stomata show some tendency to check transpiration, but the prominent palisade parenchyma denotes marked photosynthetic activity. This plant not only lives in a fairly moist habitat, but has deep roots, so that its water supply seems insured.

Rhamnaceae

Ceanothus americanus L.

Habitat: Dry, gravelly slopes.

Orientation and arrangement: Horizontal; alternate; short-petioled.

Gross structure: Ovate to oblong-ovate; somewhat pubescent.

Histology: Centric (fig. 8, plate X).

Epidermis: Thin-walled, the outer walls hardly thicker than the inner; cells small. Lower epidermis in scallops.

Stomata small; same plane with the lower epidermis.

Palisade parenchyma one layer on each side; lower layer rather irregular; occupies 2/3 parenchyma space.

Spongy parenchyma relatively large; compact; occupies 1/3 the parenchyma space.

Summary: While this plant lives in a dry, well-drained, exposed habitat, it does not show such protective characters as might be expected. Nothing is prominent except the compactness of structure. This may be accounted for by the fact that it has a relatively deep root which can reach a lower water table than the roots of some of its associates.

Umbelliferae

Eryngium yuccaefolium Michx.

Habitat: Dry soil; hill crests and slopes.

Orientation and arrangement: Ascending; stem leaves alternate; radical leaves whorled; sessile.

Gross structure: Ovate-lanceolate, cuspidate-tipped; rigid, spinose.

Histology: Centric (fig. 16, plate XI).

Epidermal outer wall 3 times as thick as inner wall; large-celled.

Palisade parenchyma one layer on each side; irregular in shape and arrangement; occupies 1/8 of parenchyma space; large-celled.

Spongy parenchyma cells elongated, their long axes at right angles to the palisade; large-celled.

Summary: Prominent large-celled photosynthetic tissue with prominent air space. Epidermal walls fairly well developed.

Primulaceae

Steironema lanceolata (Walt.) Gray.

Habitat: Alluvial basin; low, wet soil.

Orientation and arrangement: Horizontal to ascending; opposite; petioles graduated in length.

Gross structure: Lanceolate; glabrous.

Histology: Bifacial (fig. 9, plate X).

Epidermal cells large; horizontally oval; outer walls about twice as thick as inner.

Stomata slightly depressed.

Palisade parenchyma 1 layer; large, occupying 1/3 the parenchyma space.

Spongy parenchyma loose.

Summary: This leaf structure indicates the photosynthetic activity with slight conservational tendencies, as suggested by the slightly thickened outer epidermal walls and the depressed stomata.

Apocynaceae

Apocynum cannabinum L.

Habitat: Alluvial basin; wet soil.

Orientation and arrangement: Opposite, short-stemmed; horizontal to ascending.

Gross structure: Ovate to oblanceolate, glabrous or slightly pubescent.

Histology: Bifacial (fig. 10, plate X).

Upper and lower epidermis having thicker outer than inner walls. Lower epidermis scalloped, the walls in the middle of the scallops being 3 times as thick as the inner walls; outer walls curved.

Stomata small, slightly depressed; lower surface.

Palisade parenchyma 3 layers; slender; space occupied equal to that of spongy parenchyma.

Spongy parenchyma with moderate air space.

Summary: The thickenings of scallops seem practically equivalent to a uniformly thickened cuticle, for the thin places are opposite walls. This leaf shows indications of abundant water with adequate conservation facilities and a tendency to endure drought.

Asclepiadaceae

Asclepias verticillata L.

Habitat: Alluvial basin. Basal slopes or low, level, moist areas.

Orientation and arrangement: Whorled, somewhat appressed toward the stem in an upward direction.

Gross structure: Linear with revolute margins, glabrous.

Histology: Bifacial (fig. 11, plate X).

Upper epidermis twice as thick as lower, outer wall thicker than inner in both cases; walls curved.

Stomata on under surface, with thick lower walls; level with epidermis.

Palisade parenchyma two layers; broad, large, wedge-shaped cells; occupies 3/8 parenchyma space.

Spongy parenchyma twice as much as palisade, prominent air space; occupies 5/8 parenchyma space.

Summary: The slender leaves, the reflexed edges, and the thick cuticular wall indicate protective, water-retentive characters, but the abundant photosynthetic tissue with much air space would indicate sufficient available water.

Labiatae

Physostegia virginiana (L.) Benth.

Habitat: Alluvial basin; wet soil.

Orientation and arrangement: Horizontal, opposite; sessile.

Gross structure: Lanceolate to oblong; glabrous.

Histology: Bifacial (fig. 13, plate XI).

Epidermal cells moderate-sized; outer walls both about two times as thick as inner walls.

Stomata small; on the level with lower surface of epidermis.

Palisade parenchyma, cells broad; two layers, occupying about 1/2 parenchyma space.

Spongy parenchyma with large cells; much air space.

Summary: The surface stomata, the relatively thin-walled epidermis, the large-celled loose structure indicate photosynthetic activity and abundance of water without much tendency toward its conservation.

Mentha arvensis var. *canadensis* (L.) Briquet.

Habitat: Alluvial basin; damp soil.

Orientation and arrangement: Horizontal; opposite, lower leaves petioled.

Gross structure: Oblong to ovate; minutely pubescent.

Histology: Subcentric (fig. 12, plate XI).

Epidermis, both sides about equal in size, small; outer wall of upper 3 times as thick as inner wall; lower with walls of equal thickness. Upper wall with trichomes.

Stomata slightly depressed with interior cavity prominent.

Palisade parenchyma consisting of three upper and two lower layers; slender cells; occupies 3/4 parenchyma space.

Spongy parenchyma of two layers, resembling the palisade but twice as broad. Little air space.

Summary: The protective characters here seem to be the trichomes and the position of the stomata. Photosynthetic activity would seem to be prominent, according to the space provided for it.

Lycopus virginicus L.

Habitat: Alluvial basin; moist soil.

Orientation and arrangement: Ascending: petioled; opposite.

Gross structure: Ovate to ovate-oblong; puberulent.

Histology: Bifacial (figs. 14*a*, 14*b*, plate XI).

Upper epidermis thick-walled on outer side; lower epidermis uniformly thin-walled; wall of outer epidermis from a dry habitat twice as thick as that of a leaf from a moist habitat.

Palisade parenchyma 1 layer in leaves from a moist habitat; 3 layers in leaves from a dry habitat

Spongy parenchyma loose; occupies about the same space in each case, but equivalent to 2/3 the parenchyma space in the leaf from moist habitat and to 2/5 the parenchyma space in the leaf from dry habitat.

Stomata depressed in leaf of dry habitat; on level of epidermal cells in the other case.

Summary: The leaf from the dry habitat shows a thicker epidermal wall, depressed stomata and greater palisade tissues, indicating better conservational tendencies.

Scrophulariaceae

Mimulus ringens L.

Habitat: Alluvial basin; wet soil; near ponds.

Orientation and arrangement: Horizontal to ascending; sessile; clasping; opposite.

Gross structure: Oblong to lanceolate; glabrous.

Histology: Bifacial (figs. 15*a*, 15*b*, plate XI).

Variable epidermis; large-celled; fig. 15*a*, walls uniformly thin; fig. 15*b*, walls thickened on the outside.

Palisade parenchyma in fig. 15*a*, one layer; in fig. 15*b*, two layers.

Spongy parenchyma occupies about 1/2 parenchyma space in both figs. 15*a* and 15*b*, though the cells are nearly twice as long in fig. 15*a* as in fig. 15*b*.

Stomata near surface level.

Summary: Leaf shown in fig. 15*a* has no conservational devices; leaf in fig. 15*b* has evidently developed in this direction as shown by the thickened wall of the epidermis.

Compositae

Vernonia noveboracensis Willd.

Habitat: Alluvial basin; moist soil.

Orientation and arrangement: Horizontal to ascending; alternate; short-petioled.

Gross structure: Long lanceolate to lance-oblong; more or less pubescent beneath.

Histology: Subcentric (fig. 27, plate XIV).

Epidermis of uniformly thin-walled cells; mostly oblong, slightly hairy on upper surface; longer hairs on lower surface; an occasional glandular trichome on upper surface; epidermis dips down into the palisade in folds at intervals.

Palisade parenchyma loose; large-celled.

Vascular bundle surrounded by large cells, apparently water reservoirs.

Summary: Photosynthetic tissue prominent; the thin-walled epidermis contrasts with the fairly numerous trichomes on both surfaces and with the presence of water reservoirs.

Artemisia ludoviciana Nutt.

Habitat: Dry slopes.

Orientation and arrangement: Horizontal to ascending; alternate.

Gross structure: Lanceolate; upper mostly entire; lower cut-lobed, toothed, or pinnatifid; whitened woolly.

Histology: Bifacial (fig. 24, plate XIII).

Epidermal cells variable in size; thickness of walls variable, not much thicker on the outside than on the inside; trichomes numerous on both sides, but most on the upper side of leaf.

Stomata small, not much depressed.

Palisade parenchyma 2 layers, occupying 1/3 of the parenchyma space; large-celled.

Spongy parenchyma, cells large; rather loose.

Summary: Epidermal tissue not well developed except with regard to trichomes photosynthetic tissue prominent.

Aster salicifolius Ait.

Habitat: Alluvial basin; low land; moist soil.

Orientation and arrangement: Horizontal to ascending; opposite; sessile.

Gross structure: Linear to linear-oblong; glabrous, sometimes scabrous.

Histology: Centric (fig. 17, plate XII).

Outer walls of epidermis about 3 times as thick as inside walls.

Stomata on both sides.

Palisade parenchyma, 2 layers on upper, 1 layer on lower side; occupies about 2/3 the parenchyma space. Cells medium-sized.

Spongy parenchyma, cells large; fairly compact.

Summary: Epidermis with fairly well developed cuticle though with stomata on both sides; photosynthetic tissue prominent.

Coreopsis palmata Nutt.

Habitat: Prairie slopes; dry to moist.

Orientation and arrangement: Ascending; sessile; opposite.

Gross structure: Wedge shaped; lobes broadly linear; glabrous.

Histology: Centric (fig. 20, plate XII).

Epidermis of small oblong cells; the outer walls thickened, 2 to 3 times the thickness of inner ones.

Palisade parenchyma occupies 2/3 of parenchyma space; 3 layers above, 2 layers below.

Spongy parenchyma, cells large but fairly compact.

Resin ducts present.

Summary: Outer wall of epidermis fairly well developed; photosynthetic tissue prominent.

Helianthus tuberosus L.

Habitat: Slopes and level; dry to moist soil.

Orientation and arrangement: Horizontal; alternate.

Gross structure: Oblong-lanceolate; scabrous above, pubescent below.

Histology: Bifacial (fig. 18, plate XII).

Upper epidermis with outer wall twice as thick as lower; wall of lower epidermis uniformly thin, but with numerous trichomes.

Palisade parenchyma of 3 layers, occupying 1/2 the parenchyma space.

Spongy parenchyma loose.

Summary: Photosynthetic tissue prominent; prominent air space; moderate conservational tendencies.

Helianthus grosseserratus Martens.

Habitat: Dry prairie; roadsides.

Orientation and arrangement: Horizontal to ascending; petioled; alternate.

Gross structure: Elongated lanceolate to ovate-lanceolate; glabrous above; finely pubescent beneath.

Histology: Bifacial (fig. 19, plate XII).

Outer wall of upper epidermis about 3 times as thick as inner; outer wall of lower epidermis about twice as thick as inner; cells small.

Palisade, 5 layers; medium-sized, occupying 2/3 of parenchyma space.

Spongy parenchyma loose.

Summary: Epidermal tissue better developed in *H. grosseserratus* than in *H. tuberosus.* Photosynthetic tissue is more compact.

Silphium laciniatum L.

Habitat: Rather dry priarie; sometimes moist slopes.

Orientation and arrangement: Stem leaves ascending; lower and root leaves vertical; alternate; petioled.

Gross structure: Pinnately parted, lobes lanceolate or linear, cut-lobed or pinnatifid; rough-bristly.

Histology: Subcentric (young leaf) (fig. 22, plate XII).

Epidermal cells square; with outer wall of epidermis 4 to 5 times as thick as inner wall.

Palisade in 5 layers, the longest at the top; fairly compact.

Summary: The well cuticularized epidermis indicates the ability to modify transpiration, while the prominent palisade implies pronounced photosynthetic activity.

Solidago rigida L.

Habitat: Dry soil; ridges and hillsides.

Orientation and arrangement: Ascending, somewhat appressed; petioled; upper leaves sessile.

Gross structure: Oval or oblong; rough-hoary with minute pubescence.

Histology: Concentric (fig. 26, plate XIV).

Epidermal cells small with outer walls 3 times as thick as inner; trichomes on both sides.

Stomata on both sides.

Palisade parenchyma, 3 layers on upper and 2 on lower side; loose; occupies 2/3 the parenchyma space.

Spongy parenchyma, small-celled; loose.

Stomata small, level with lower edge of epidermis.

Summary: Epidermis well equipped for conservation of water with the exception of stomata. Solereder states that stomata are often found on the upper sides of appressed leaves from dry habitats. Photosynthetic tissue well developed with prominent air space.

Solidago serotina Ait.

Habitat: Moist soil; slopes.

Orientation and arrangement: Horizontal to ascending, somewhat appressed; sessile.

Gross structure: Lanceolate to oblanceolate; glaucous.

Histology: Bifacial (fig. 23, plate XIII).

Epidermis of irregular-sized cells, convex-walled; outer wall about 1 1/2 times as thick as inner.

Stomata on level with lower edge of the epidermis.

Palisade parenchyma, 2 layers; broad-celled.

Spongy parenchyma, large-celled; rather loose; occupies 2/3 of parenchyma space.

Resin ducts present.

Summary: Has facilities for marked photosynthetic activity with slight protective device.

Solidago canadensis L.

Habitat: Moist soil; slopes.

Orientation and arrangement: Ascending, somewhat appressed; sessile.

Gross structure: Leaves narrowly lanceolate; glabrous above; minutely pubescent below.

Histology: Centric (fig. 25, plate XIII).

Epidermis thicker on upper than on lower side; outer walls about twice as thick as inner; trichomes on lower epidermis.

Stomata on both sides.

Palisade, 2 layers on upper surface and 1–2 on lower surface, occupying 2/3 the parenchyma space.

Spongy parenchyma of elongated cells running at right angles to the palisade; compact.

Resin ducts present.

Summary: A typical sun leaf with moderately developed protective devices to provide for active photosynthesis. Consistent with its moderately moist habitat.

Solidago graminifolia (L.) Salisb.

Habitat: Alluvial basin; moist soil.

Orientation and arrangement: Horizontal to ascending; sessile.

Gross structure: Lance-linear; glabrous.

Histology: Centric (fig. 21, plate XII).

Epidermal cells small; outer wall 1/3 thicker on upper than on lower side; outer wall of upper epidermis 3 times as thick as inner.

Palisade parenchyma, one layer on each side; cells rather small, oval; occupies 1/2 parenchyma space of leaf.

Spongy parenchyma cells large; fairly compact.

Summary: Leaf fairly thin without trichomes or prominent protective device; well developed palisade and spongy parenchyma.

Comparison of Leaf Anatomy of Upland and Alluvial Basin Plants

The following plants were selected from two formations:

I. Prairie hill crest and slope: *Andropogon scoparius*, *Bouteloua curtipendula*, *Anemone cylindrica*, *Amorpha canescens*, *Ceanothus americanus*, *Eryngium yuccaefolium*, *Artemisia canadensis*, *Solidago canadensis*, *Solidago rigida*, *Coreopsis palmata*, *Helianthus grosseserratus*, *Helianthus tuberosus*.

Epidermis. Of these twelve upland plants, all have a relatively thick outer-walled epidermis, or prominent trichomes if the wall is not thick. The presence of trichomes may be regarded as an anatomical equivalent of thick-walled epidermis. Two have prominent bulliform cells and vascular bundles. (Not enough data are recorded for stomata to warrant comparisons.)

Parenchyma:

Subcentric leaves.

(1) Five layers palisade parenchyma.

(2) Four layers palisade.

Centric.

(1) Three upper, two lower layers palisade; spongy parenchyma loose.

(2) Three upper, two lower layers palisade; spongy parenchyma large-celled, compact.

(3) One upper, one lower layer palisade; spongy parenchyma large-celled, compact.

(4) One upper, one lower layer palisade; spongy parenchyma horizontally elongated.

Bifacial.

(1) Two layers of palisade cells; spongy parenchyma cells compact, small.

(2) Two layers of palisade cells; spongy parenchyma cells large, compact.

(3) Three layers of palisade cells; spongy parenchyma cells loose, elongated.

(4) Four layers of palisade cells; spongy parenchyma cells loose, elongated.

Radial palisade.

(1) Radial palisade; spongy parenchyma homogeneous.

(2) Radial palisade; spongy parenchyma homogeneous.

II. Alluvial basin: *Leersia oryzoides*, *Muhlenbergia mexicana*, *Polygonum Muhlenbergii*, *Baptisia leucantha*, *Steironema lanceolata*, *Asclepias verticillata*, *Apocynum cannabinum*, *Mimulus ringens*, *Lycopus virginicus*, *Mentha canadensis*, *Physostegia virginiana*, *Solidago serotina*, *Solidago graminifolia*, *Vernonia noveboracensis*, *Silphium laciniatum*, *Aster salicifolius*.

Epidermis: Of the sixteen alluvial basin plants examined, nine have a lower epidermal wall relatively thinner than that on the upper side. Ten are smooth.

Parenchyma:

Subcentric.

(1) Five layers palisade.

(2) Six layers palisade.

(3) Seven layers palisade.

Centric.

(1) One upper, two lower layers palisade; spongy parenchyma compact.

(2) Two upper, two lower layers palisade; spongy parenchyma compact.

Bifacial.

(1) One layer palisade; spongy parenchyma loose.
(2) One layer palisade; spongy parenchyma loose.
(3) Two layers palisade; spongy parenchyma loose.
(4) Two layers palisade; spongy parenchyma loose.
(5) One-two layers palisade; spongy parenchyma loose.
(6) Three layers palisade; spongy parenchyma loose.
(7) One-three layers palisade; spongy parenchyma loose.

Homogeneous.

(1) Rather compact mesophyll (Grass).
(2) Rather compact mesophyll (Grass).

Mimulus ringens studied in two habitats shows in one location two layers of palisade and a relatively thick outer epidermis, while in the moister habitat it has a uniformly thin epidermis and one layer of palisade with a thicker area of spongy parenchyma.

Polygonum Muhlenbergii shows a development of trichomes and a thicker palisade in leaves growing a few rods from a pond, while in shallow water its leaves are smooth and have a narrower palisade.

The Compositae and Gramineae by far exceed the other families in both number of representative species and individuals thereof.

Compositae. The Compositae show considerable variation of tissues, but are characterized by prominent palisade, four of the leaves having a centric structure, two subcentric, and four bifacial with deep palisade. The spongy tissue where present is loose. On low, wet land trichomes are generally not developed. Thickened epidermal walls are representative. The leaves are characterized by intensive photosynthetic activities. A tissue may be represented by an anatomical equivalent under different conditions indicating adaptability to habitat, manifested not only in anatomical characters but through evidence of wide distribution and great numbers.

All these Solidagos have well developed palisade but each of a different type. *S. rigida* has the driest habitat and shows the most prominent palisade, cuticle, and trichome development. The leaves appressed to the stem are associated with the presence of stomata on both sides. *S. serotina* has a moist habitat and shows practically no protective devices, having epidermal walls with loose spongy parenchyma. *S. graminifolia*, though growing in as moist, if not a moister, habitat than *S. serotina*, has a thicker cuticle and more compact parenchyma with two layers of palisade. *S. canadensis* has a fairly dry habitat though not so dry as that of *S. rigida*. Its compact tissue, prominent palisade, and thick-walled hairy epidermis seem consistent with its location.

Gramineae. The grasses of the lowland show a thinner epidermis, fewer and smaller bulliform cells, and less specialized palisade in the alluvia

basin than in the upland prairie. Among the contributions dealing with Iowa grasses are the following: Emma Pammel Hansen (12) studied the anatomy of *Lolium perenne*, *Festuca elatior*, *F. tenella*, and *Bromus patulus*. Emma Sirrine (17) described and illustrated the anatomy of *Bromus patulus*, *B. inermis*, and *B. secalinus*. Pammel and Sirrine (13) investigated the anatomy of *Sporobolus heterolepis*, *S. cryptandrus*, *S. Hookeri*, *S. vaginaeflorus*, *Panicum capillare*, *P. proliferum*, and *P. crusgalli*. These investigators call attention to the difference in anatomy of plants growing in dry and in humid environments. C. R. Ball (2) examined *Eragrostis reptans*, *E. pectinacea*, *E. Purshii*, *E. Frankii*, *E. Mexicana*, and *E. major*, and describes the epidermal cells of *E. pectinacea* as having thicker walls than those of *E. Purshii*, the latter being adapted to dry and sandy soil. C. B. Weaver (21) worked upon the anatomy of *Andropogon nutans*, *A. scoparius*, *A. sorghum*, and *A. sorghum* var. *halepense*. Miss Pammel's studies of Bromus show little development of bulliform cells and a homogeneous mesophyll, in contrast with the prominent bulliform cells of reduced spongy parenchyma and the radial palisade of Weaver's Andropogon and Ball's Eragrostis, both species of dry habitats. Theo. Holm (8) has studied the species of the genera Uniola, Distichlis, Pleuropogon and Leersia. Pammel, Weems, and Lamson-Scribner (11) have called attention not only to the use of anatomical characters of grasses for systematic distinction but to such structures as related to habitat. An interpretation of the above cited morphological facts concerning a number of species of a genus and a comparison of genera with a knowledge of the habitats of these plants would leave no doubt as to the adaptation of species of this family to their habitats.

In general, the anatomy of these leaves of prairie plants resembles that of the plants described in Harshberger's (7) pine barren studies in their development of epidermis and mesophyll features.

Ella Shimek (16) has described plants of Iowa prairies with some illustrations of leaf characters, in which the leaf structure coincides with the anatomical observations of the present study.

Summary

The leaves of prairie plants show a xerophytic tendency in their leaf structure, indicated by the specialized palisade tissue, the thick-walled and trichomeless epidermis, the presence of water-storing tissue, and sometimes of trichomes.

The mere presence of these characters is not of primary significance as an indication of xerophytism. but their relative development correlated with other morphological features of the plant such as the extensiveness of the root system.

The upland plants have a thinner epidermis than those of the lowland, and 70 percent of those studied are without trichomes while 75 percent of the upland species have trichomes.

Of the alluvial basin leaves studied, 50 percent were bifacial while 33 percent of the upland plants have bifacial leaves; 12½ percent of the alluvial basin plants were centric to subcentric; 50 percent of the upland plants were centric to subcentric.

Iowa State College,
Ames, Iowa

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EXPLANATION OF PLATES IX-XIV

The figures were made with the aid of a camera lucida and are magnified approximately 30 diameters.

Ed, dorsal epidermis; *Ev*, ventral epidermis; *P*, palisade parenchyma; *Sp*, spongy parenchyma; *VB*, vascular bundle; *b*, bulliform cell; *r*, resin duct; *s*, stomate; *t*, trichome; *cps*, chlorophyll parenchyma sheath.

PLATE IX. Fig. 1, *Andropogon scoparius;* Fig. 2, *Bouteloua curtipendula;* Fig. 3, *Muhlenbergia mexicana;* Fig. 4, *Leersia oryzoides;* Fig. 5, *a* and *b*, *Polygonum Muhlenbergii;* Fig. 6, *Anemone cylindrica.*

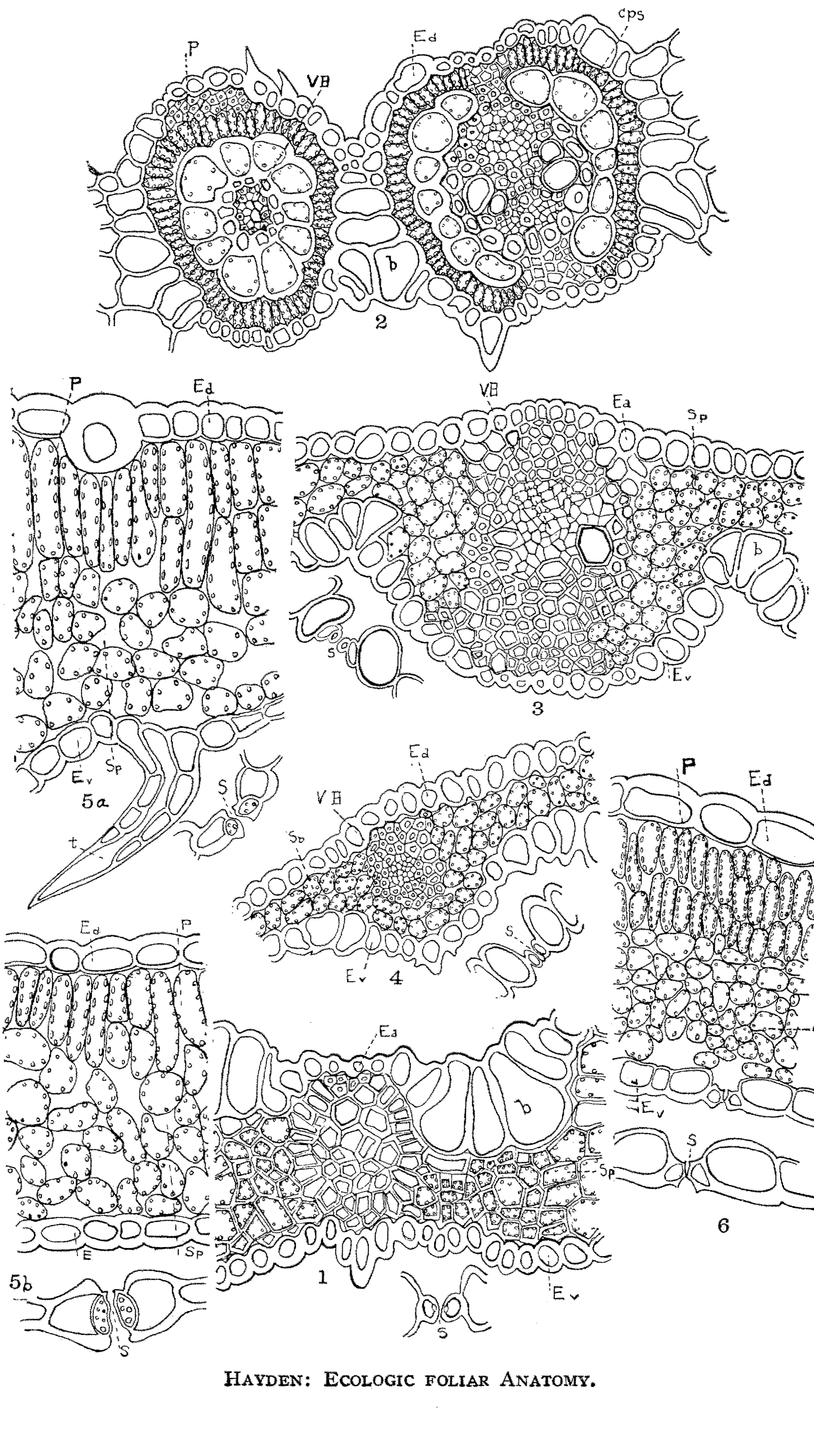
PLATE X. Fig. 6*a*, *Baptisia leucantha;* Fig. 7, *Amorpha canescens;* Fig. 8, *Ceanothus americanus;* Fig. 9, *Steironema lanceolata;* Fig. 10, *Apocynum cannabinum;* Fig. 11, *Asclepias verticillata.*

PLATE XI. FIG. 12, *Mentha arvensis* var. *canadensis;* Fig. 13, *Physostegia virginiana;* Fig. 14, *a* and *b*, *Lycopus virginicus;* Fig. 15, *a* and *b*, *Mimulus ringens;* Fig. 16, *Eryngium yuccaefolium.*

PLATE XII. FIG. 17, *Aster salicifolius;* Fig. 18, *Helianthus tuberosus;* Fig. 19, *Helianthus grosseserratus;* Fig. 20, *Coreopsis palmata;* Fig. 21, *Solidago graminifolia;* Fig. 22, *Silphium laciniatum.*

PLATE XIII. Fig. 23, *Solidago serotina;* Fig. 24, *Artemisia ludoviciana;* Fig. 25, *Solidago canadensis.*

PLATE XIV. Fig. 26, *Solidago rigida;* Fig. 27, *Vernonia noveboracensis.*



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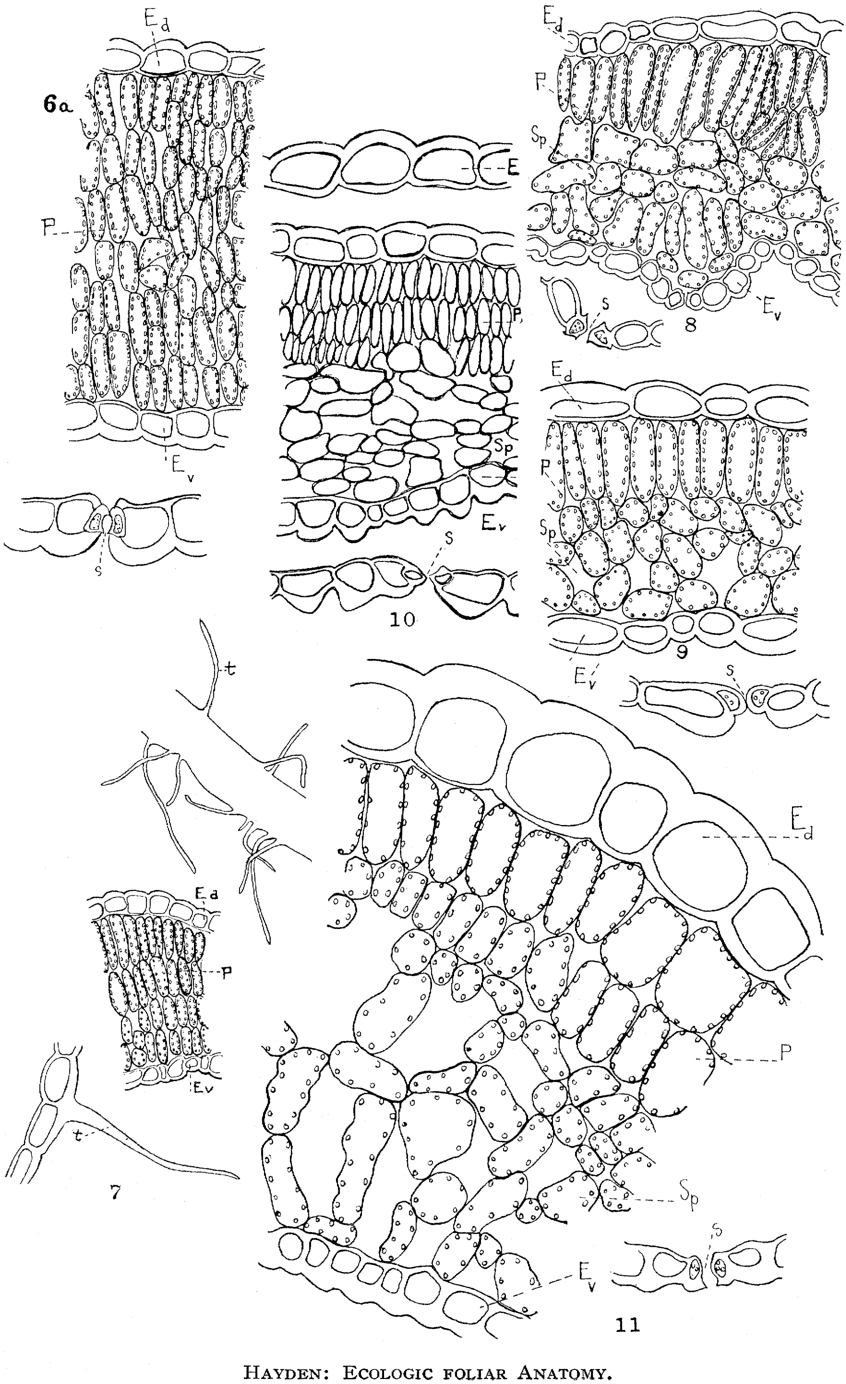

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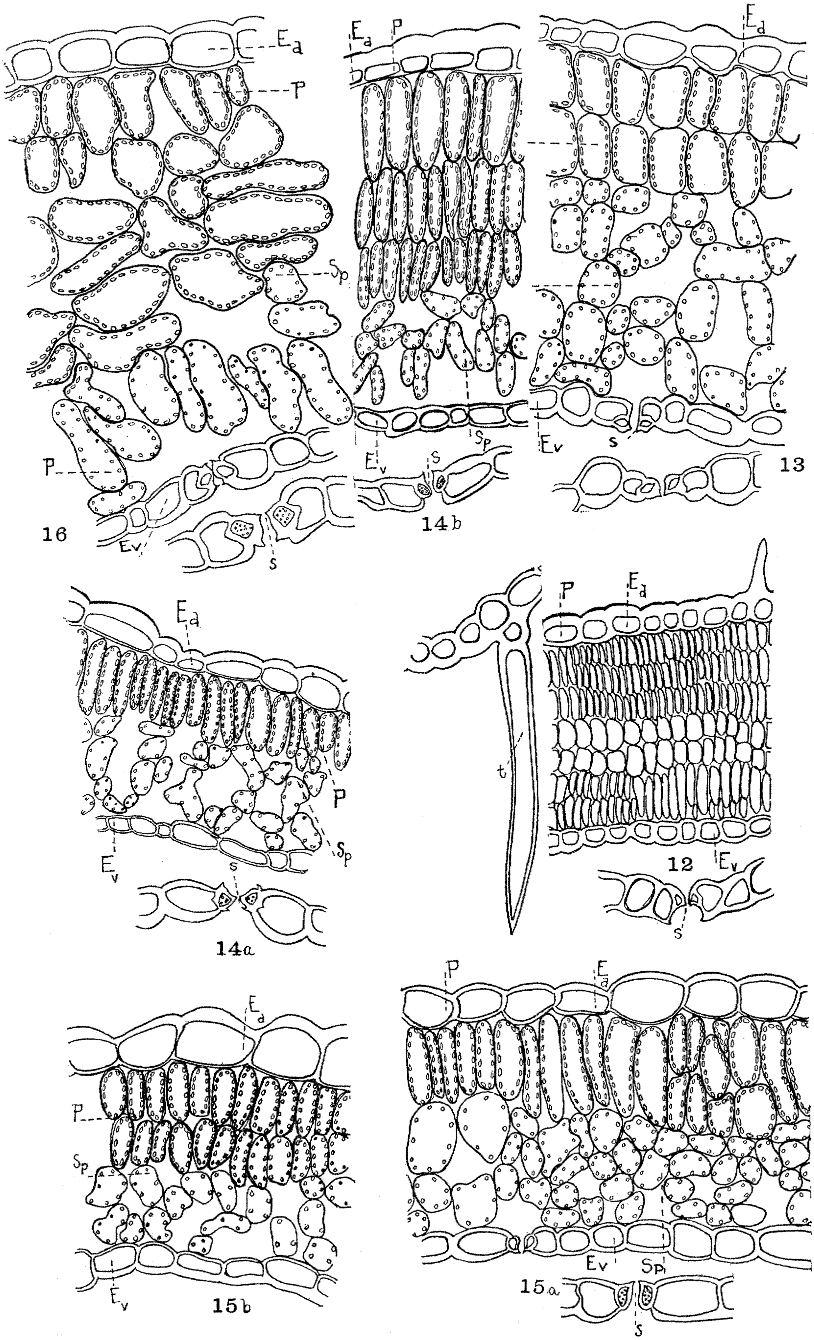

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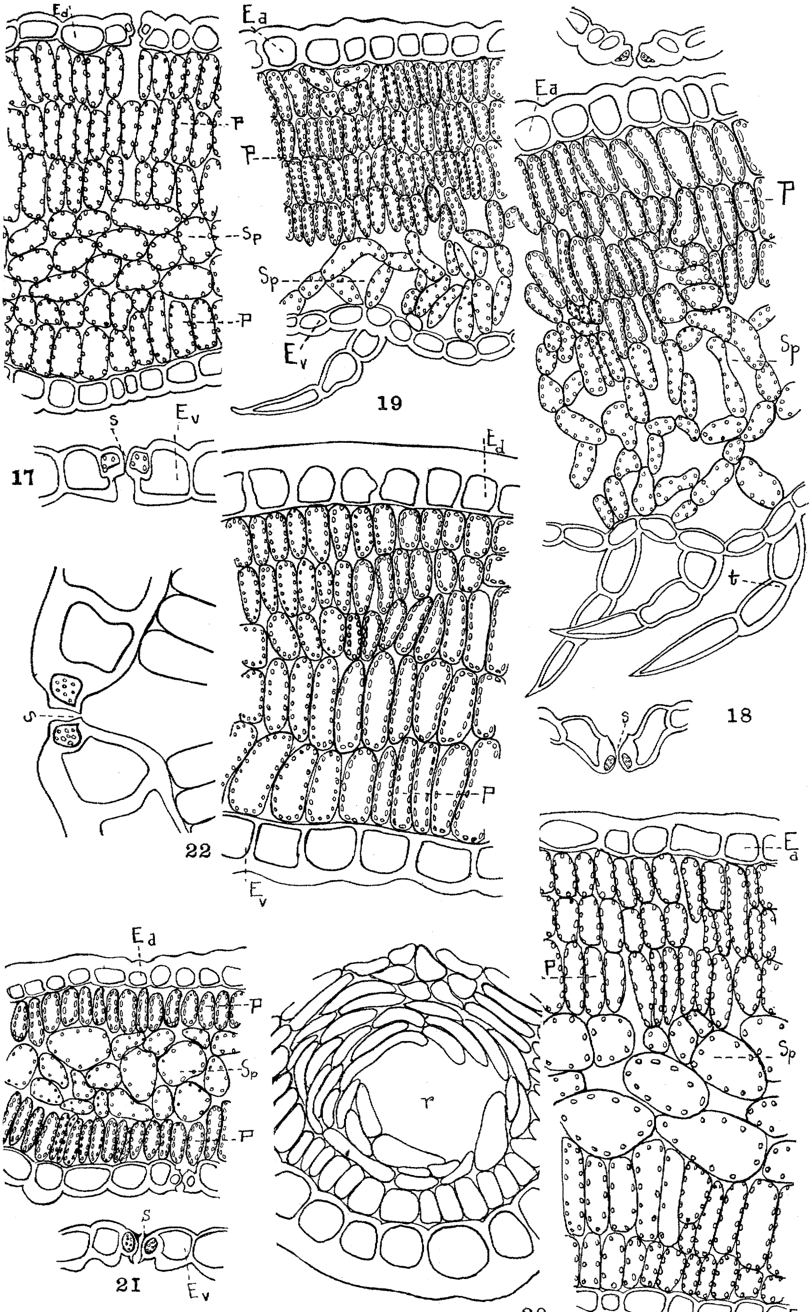

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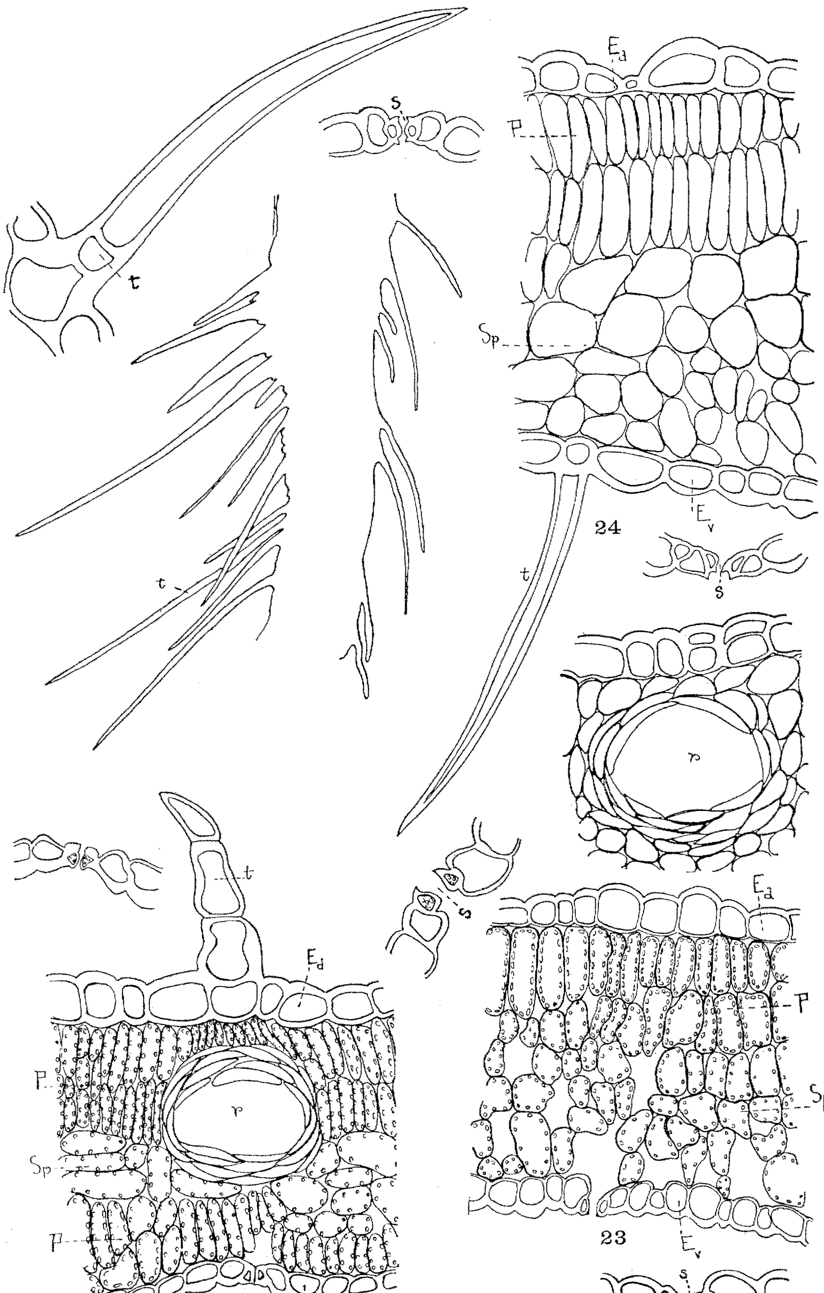

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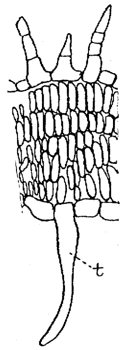

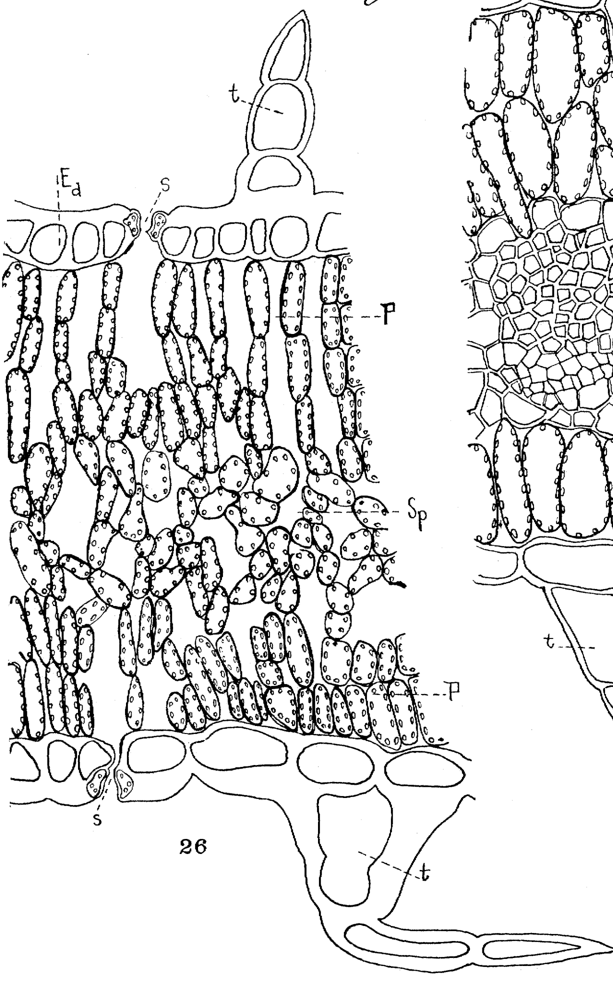

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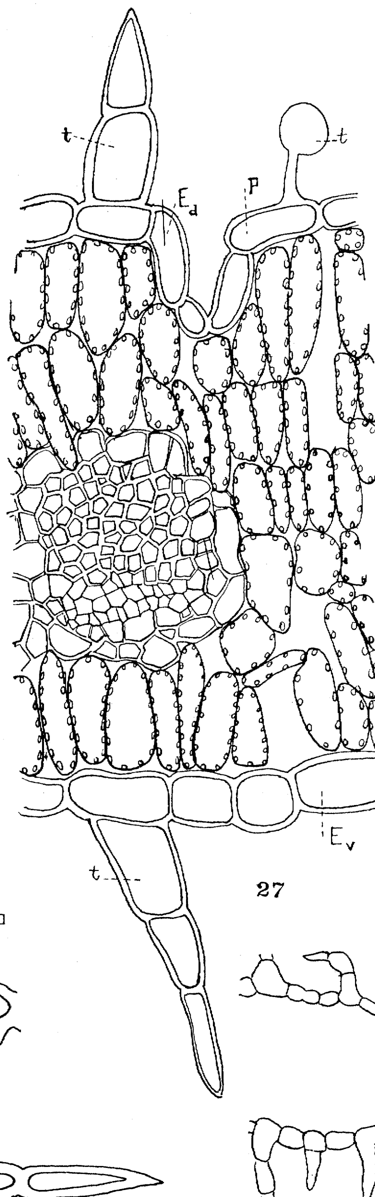

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